

Observations on two large athecate hydroids (Cnidaria: Hydrozoa) from the Kamchatka Peninsula (NW Pacific)

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Abstract

This study reports on several specimens of two large hydroids from the North-Western Pacific Ocean: *Monocoryne bracteata* and *Candelabrum phrygium*. Both species are documented with photographs of the living animals as well as with photographs of the nematocysts and histological sections of the sporosacs. Both are rare animals and only known from a few specimens, which makes it difficult to assess their intraspecific variation. The new material differs in some minor details from previously known material and the significance of this is discussed here. It is concluded that these differences likely represent intraspecific variation. A re-examination of type material of *Candelabrum verrucosum* Bonnevill, 1898 added to knowledge of this nominal species and provided evidence that it is conspecific with *C. phrygium*. The diagnostic feature “nematocyst buttons on the sporosacs” of *C. verrucosum* occurs also in otherwise typical *C. phrygium* identified by other authors.

Keywords: Anthoathecata - Aplanulata - Capitata - systematics - biology - *in situ* observations - 16S sequence.

INTRODUCTION

Although ubiquitous in the marine environment, most hydroid polyps are small to microscopic. As a result, they tend to be noticed in the field only when colonies are formed. Nevertheless, a few hydroid polyps can grow to large sizes, with *Branchiocerianthus imperator* (Allman, 1885) reaching 1 metre or more (Schuchert, 2010), or *Candelabrum penola* reaching 85 cm in height (Manton, 1940). Other more common macroscopic hydroids include members of the families Tubulariidae and Corymoridae. Because solitary macroscopic hydroid polyps are seen infrequently, two of us (N.S. and K.S.) were immediately aware of their uniqueness when we discovered two different species of conspicuous polyps while diving in waters of the Kamchatka Peninsula (NW Pacific Ocean). Their size and considerable numbers made it possible for us to take *in situ* photographs and to collect them individually for more detailed examination. The two species clearly belonged to the genera *Monocoryne* and *Candelabrum*. However, identification of them to species rank was difficult, and our taxonomic investigations and comparisons are presented in this work. For both genera, the extent of intraspecific morphological variation is difficult to assess due to the

current paucity of information. Only the accumulation of data through published studies on different populations will enable us to acquire a clearer idea of the intra- and interspecific variation of these animals. *Monocoryne* in particular is a rare, poorly-known genus, and more detailed information about its species is desirable. Except for *C. cocksii*, all other species of *Candelabrum* are also rare and few records of them exist.

MATERIAL AND METHODS

Hydroids studied here were observed, photographed and collected using SCUBA. Material for museum collections were preserved initially in 4% formaldehyde and subsequently transferred to 70% ethanol. Specimens for DNA extraction were preserved in absolute ethanol. For morphological examination techniques and terms see Schuchert (2012). Histological serial sections were made using standard paraffin embedding procedures, followed by haematoxylin and eosin staining. Nematocyst examinations and identifications were done using pieces of material preserved in absolute ethanol examined either in water or 50% lactic acid.

DNA extraction and sequencing of part of the 16S

mitochondrial RNA gene were done as described in Schuchert (2005; 2014). The DNA samples are in the DNA collection of the MHNG.

Photographs of type specimens of *Monocoryne bracteata* were provided by Dr Allen Collins (National Museum of Natural History, Washington), and those of the holotype of *C. serpentarii* were provided by Dr A. Andouche (Muséum National d'Histoire Naturelle, Paris).

Loans of specimens were provided by ROMIZ, ZMUC, and UZMO (see under material examined).

Museum acronym abbreviations:

- MHNG Muséum d'histoire naturelle, Genève, Switzerland
 ROMIZ Royal Ontario Museum, Invertebrate Zoology, Canada
 UZMO Zoological Museum of the University of Oslo, Norway
 ZIRAS Zoological Institute of the Russian Academy of Sciences
 ZMUC Zoological Museum of the University of Copenhagen, Denmark

TAXONOMY

Monocoryne bracteata (Fraser, 1943)

Figs 1-3

Symplectanea bracteata Fraser, 1943: 78, pl. 13 fig. 1.

Monocoryne bracteata. – Rees, 1958: 17, fig. a-b. – in part Stepanjants *et al.*, 2003: figs 2A & 2C. – Brinckmann-Voss & Lindner, 2008: 1634, fig. 2A-B.

Material examined:

- MHNG-INVE-92014, field number Kam05; 15 specimens in ethanol (males and females) and serial histological sections of middle region of males and females; Russia, Kamchatka Peninsula, Avacha Bay, Starichkov Island, 52.7823°N 158.61575°E, 16 m depth, temperature 2°C; collection date 18.06.2014; DNA extracted from 2 specimens preserved in ethanol, DNA isolates 1123 and 1124 gave both the same 16 sequence LN898142.
- MHNG-INVE-92015, field number Kam06; 1 male and 1 female specimen in ethanol; Russia, Kamchatka Peninsula, Starichkov Island, 52.77915°N 158.61268°E, 7 m depth, temperature 10 °C; collection date 24.06.2009.
- MHNG-INVE-92016, field number Kam07; 9 specimens in ethanol, males and females; Russia, Kamchatka Peninsula, Starichkov Island, 52.7796°N 158.6111°E, 10 m depth, temperature 5°C; collection date 17.07.2009; DNA extracted from 2 specimens preserved in ethanol, DNA isolates 1125 and 1126 gave both the same 16S sequence LN898143.

ZIRAS; several specimens in ethanol, one with branched polyp body; Russia, Kamchatka Peninsula, Avacha Bay, Starichkov Island, on pebbles, 52.7790°N, 158.6124°E, 8 m depth, temperature 4°C; collection date 02.06.2011.

ROMIZ B3646, 1 fragmented specimen with female sporosacs in ethanol; Russia, Okhotsk Sea, Urup Island, 46°N 149°E, 300 m depth; collection date 07.08.1987; elongate sporosacs with 0-20 egg like bodies.

Type locality: Albatross Station 4253; 57.67194°N 133.67944°W, Thistle Ledge, Stephens Pass, south-eastern Alaska, water depth 240-344 m (Brinckmann-Voss & Lindner, 2008).

Diagnosis: Solitary species of *Monocoryne*, with or without anchoring filaments, up to 200 widely spaced tentacle-groups comprising 3-10 tentacles (mostly around 6), tentacles grouped in linear arrays. Individuals gonochoristic, gonophores developing in upper axis of tentacle-groups, occurring as sporosacs without canal systems, elongate when fully mature, up to 3-4 times as long as wide, mature females with 3-20 maturing oocytes.

Description of Kamchatka material:

Morphology: Hydroid polyps solitary, vermiform, able to contract to 1/10 of length, not gregarious, subdivided into a basal, tentacle-free foot and an upper, tentacle-bearing part. Foot conical, length about 1/6 or less of total height when expanded, up to 1/3 when contracted or preserved, sheathed in an adhering, very thin, filmy perisarc, hardly visible in living animals, loose and wrinkled in preserved specimens. Basal tip of perisarc attached directly to substrate (small stones, shell debris); anchoring filaments absent. Tentacle-bearing zone thin, vermiform, squirming, beset with widely spaced groups of tentacles (in relaxed body). Tentacles capitate, somewhat contractile, up to 200 or more, in groups of 3-10 (mostly around 6), those of a cluster in a single row with bases fused through a common epidermis (Fig. 2G), rows of tentacles oriented transversely or obliquely to polyp axis. Terminal knobs (capitula) of tentacles spherical, about twice diameter of stalk; tentacle stalks relatively long and thin when extended. Terminal region of polyp with small, shallow hypostome surrounded by solitary tentacles.

Gonophores sporosacs developing singly in upper axils of tentacle-groups, usually confined to lower half of tentacle-bearing part. Sporosacs with distinct spadix, without radial canals or other vestiges of medusa stage (Fig. 2E-F). Young sporosacs spherical, later becoming elongated, contractile. Fully developed, relaxed male sporosacs oblong, about three times as long as thick (Fig. 2B). Female sporosacs spherical to spindle shaped when mature (Fig. 2C-D), containing 1-4 white, egg-like bodies (mature oocytes or clusters of developing oocytes and their nourishing cells). Individual polyps apparently either male or female, never hermaphroditic.



Fig. 1. *Monocoryne bracteata*, living animals, all Kam07. (A) Whole, expanded polyp, size about 3-4 cm. (B) Fully contracted polyp. (C) Tentacles, note clustering in linear arrays and fusion of bases.

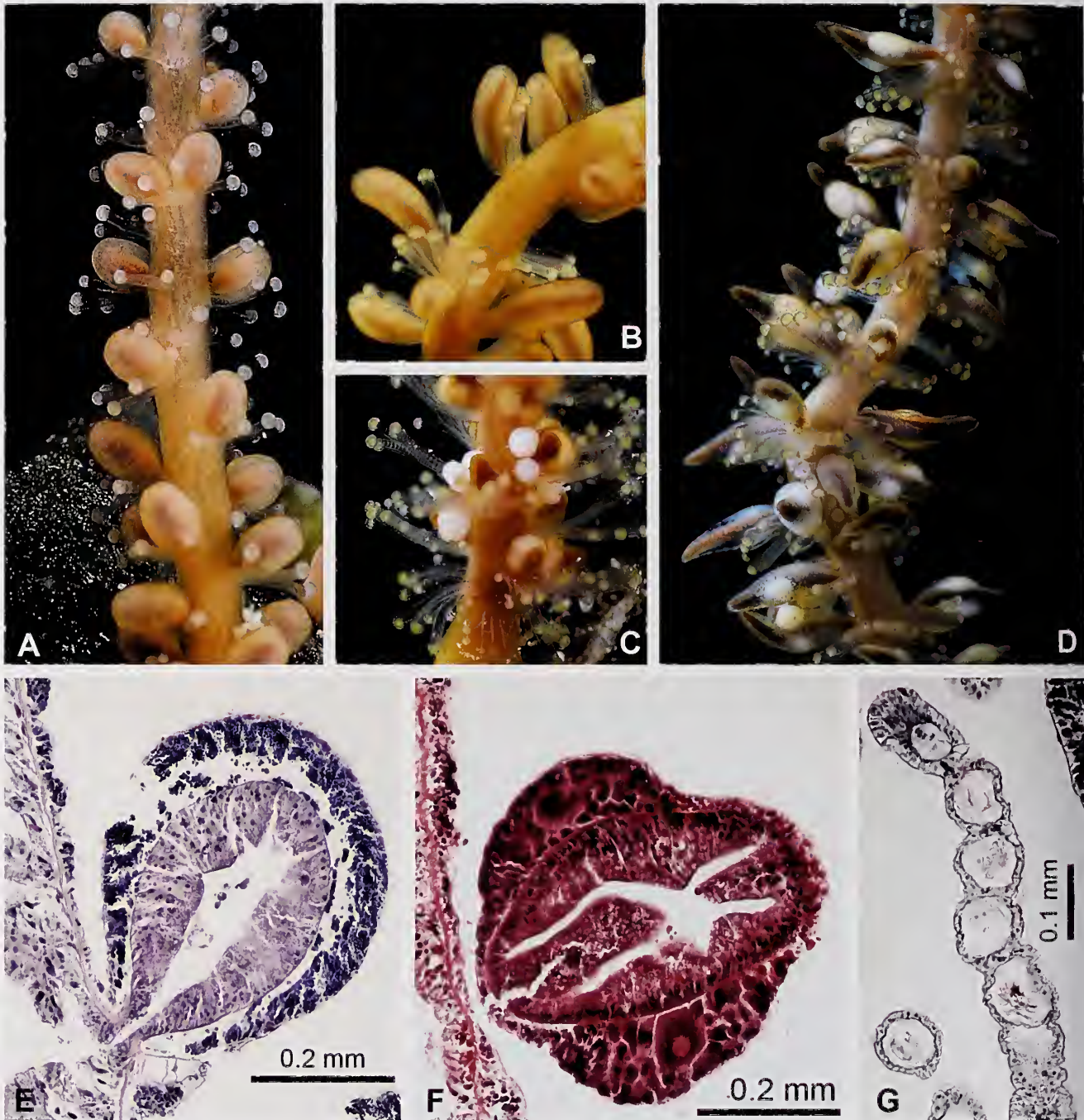


Fig. 2. *Monocoryne bracteata*, living animals, except E-G. (A) Young male sporosacs, Kam05. (B) Mature male sporosacs, Kam06. (C-D) Mature female sporosacs, likely after partial spawning, Kam06. (E) Longitudinal section through mature male sporosac, Kam05. (F) Longitudinal section through female sporosac with two growing oocytes surrounded by nourishing cells which will later fuse with the oocyte; Kam05. (G) Transverse section near the base of a tentacles group, note linear arrangement and shared epidermal layer.

Nematocysts (preserved tissue): Larger stenoteles (10.5-13) \times (14-15) μm ; smaller stenoteles (8-9) \times (11.5-13) μm ; desmonemes (5-6.5) \times (7-9) μm ; microbasic heteronemes (5-6.5) \times (13.5-18) μm (Fig. 3A-D).

Dimensions: Fully grown expanded polyp 40 mm and more, diameter ca. 0.8 mm; preserved specimens about 10-15 mm. Expanded tentacles up to 1.5 mm long.

Sporosacs 0.8-2.1 mm long. Eggs maximally 0.35-0.5 mm in size.

Colours: Variable, yellowish-orange (Fig. 1A-B), pale-pink-orange, to orange-red. Surface of sporosac sometimes with rusty-red pigment clusters (Fig. 1B). Spadices of sporosacs when fully grown dark brown-red, eggs white when fully mature (Fig. 2C-D).



Fig. 3. *Monocoryne bracteata*, (A-D) Nematocysts of material preserved in 100% ethanol, Kam05, scale bar 10 µm valid for all images. (A) Stenoteles. (B) Desmonemes. (C) Microbasic heteronemes. (D) Shafts of discharged microbasic heteronemes. (E) Preserved specimens, all Kam05.

Other observation: One polyp with a bifid, Y-shaped body was found.

Biology: Found in depths of 7-16 m in gravel, attached to small stones, shell debris, or tubes of polychaetes.

Distribution: North Pacific; South-eastern Alaska (Fraser, 1943), Kamchatka Peninsula and Urup Island (this study), depth range 7-344 m.

Remarks: Hydroids of *Monocoryne* Broch, 1910, rare and seldom observed, are rather distinctive in having a large, worm-like body with numerous tentacles that are usually clustered in linear groups (Fig. 1A). Currently comprising four species (Schuchert, 2015), the genus has recently been reviewed by Stepanjants *et al.* (2003). Since that review, a new species (*Monocoryne colonialis*) has been described by Brinckmann-Voss & Lindner (2008) that had previously been mistaken by Stepanjants *et al.* for *M. bracteata*. One species of the genus, *M. minor* Millard, 1966, is restricted to South Africa. Meanwhile, *M. colonialis* is unusual in forming small colonies and in having tentacles that are

not in groups. These two species can be excluded from consideration in identification of the present material. The two remaining species, the Atlantic *M. gigantea* (Bonnevie, 1899) and the Pacific *M. bracteata* (Fraser, 1943) appear to be very similar morphologically. After examining type material of both species, Rees (1958) concluded that they could be conspecific. He kept them apart only because the type material of *M. bracteata* was in such a poor condition that it precluded any appropriate comparison. Both species are rare, *M. bracteata* was so far only known from type material consisting of two fragmented polyps. Apart from their geographic origin (Atlantic- versus Pacific Ocean), the two are currently only distinguished based on the maximal number of tentacles per cluster ("bract-like" clusters of Fraser, 1943), with 3-4 in *M. gigantea* and 4-7 in *M. bracteata* (Rees, 1956, 1958; Brinckmann-Voss & Lindner, 2008).

Rees (1958) claimed that *M. bracteata* might have hermaphroditic sporosacs as in *M. gigantea* (see Johannesen, 1924). However, he did not make histological

sections and without them, sex determination in preserved hydroids is difficult. Preserved Kamchatka samples were impossible to sex unambiguously without histological sections. Photos of the type specimen of *M. bracteata* show sporosacs with a few (4-5) egg-like bodies only, although Brinckmann-Voss & Lindner (2008) depict 7 in their drawing. Fraser (1943) shows many more, but his drawings tend to be somewhat inaccurate and his text states that they are “not numerous”. The sample from Urup Island likewise had sporosacs with spindle-shaped spadices surrounded by 8-20 egg-like bodies (max. size 0.3 mm). However, a few sporosacs had no eggs at all and had presumably spawned already. It is therefore assumed that the low egg numbers per sporosac observed in the Kamtchaka material (Fig. 2C-D) is due to older sporosacs that had already liberated eggs. What appears as eggs in female sporosacs are often only clusters of nourishing cells surrounding a developing oocyte (Fig. 2F). Egg numbers per sporosac in *M. gigantea* are not known, but illustrations in Johannesen (1924) suggest low numbers as in *M. bracteata*.

The histological examinations (Fig. 2E-F) showed that the Kamchatka animals are clearly dioecious, in contradistinction to *M. gigantea* which is hermaphroditic (see Johannesen, 1924). This should be taken as a species specific difference.

As for the cnidome, the heteronemes (Fig. 3D) might be interpreted as microbasic euryteles with a faint swelling, but as is often the case in studies of preserved material they could be mastigophores instead.

The four 16S sequences obtained from *M. bracteata* were all either very similar or identical, adding further evidence that all the samples belong to the same species. The sequences are rather distant to all other Hydrozoa 16S sequences, but similar to an unpublished 16S sequence of *Monocoryne colonialis* (results not shown). To conclude, the numerous polyps from the Kamchatka Peninsula examined here most likely belong to *M. bracteata*, despite the following differences from the type specimens:

- shallow water (7-16 m) versus deep-water (>240 m)
- no attachment filaments; shorter foot region (2/3 of total height in type)
- fewer eggs per sporosac
- shape of fully grown sporosac more elongated.

The deep water specimen from Urup Island more closely resembles the type material of *M. bracteata*. All these differences were interpreted here as a combination of

intraspecific, environmentally induced, and age-related variations.

Candelabrum phrygium (Fabricius, 1780)

Figs 4-6, 7E-F

Lucernaria phrygia Fabricius, 1780: 343.

Myriothela arctica M. Sars, 1850: 134.

Myriothela phrygia. – M. Sars, 1877: 23, pl. 2 figs 29-36. – Bonnevie, 1899: 35, pl. 4 figs 5-6. – Jäderholm, 1908: 9, pl. 1 fig. 7. – Broch, 1916: 19, fig. C, pl. 1 figs 3 & 8. – Rees, 1957: 486, fig. 36. – in part Naumov, 1969: 261, not figures [= *C. cocksii*]. – Calder, 1972: 222, pl. 1 fig. 5.

? *Myriothela gigantea* Bonnevie, 1898: 490, pl. 27 figs 46-47. – Bonnevie, 1899: 38, pl. 4 fig. 1. – Rees, 1956: 115, synonym.

? *Myriothela minuta* Bonnevie, 1898: 489, pl. 27 fig. 44. – Bonnevie, 1899: 37, pl. 3 fig. 6a-b, pl. 4 fig. 4. – Rees, 1956: 115, synonym.

? *Myriothela mitra* Bonnevie, 1898: 489, pl. 27 fig. 43. – Bonnevie, 1899: 38, pl. 3 fig. 6c-e, pl. 4 fig. 3. – Rees, 1956: 115, synonym.

Myriothela verrucosa Bonnevie, 1898: 468, pl. 27 fig. 45. – Bonnevie, 1899: 37, pl. 4, fig. 2 & 2a. – Rees, 1956: 115, synonym.

Candelabrum phrygium – in part Cornelius, 1977: 521 [excl. synonymy]. – Segonzac & Vervoort, 1995: 45, figs 2e-f, 3E-F, table 1 [some references do not refer to this species]. – Schuchert, 2001: 37, fig. 24. – Schuchert, 2006: 346, fig. 8. – Antsulevich, 2015: 176, fig. 78A-B. not *Myriothela phrygia*. – Hincks, 1868: 77. – Allman, 1874: 317. – Allman, 1875a: 135. – Allman, 1875b: 250. – Allman, 1875b: 317. – Allman, 1876: 549, pls 55-58. – Hardy, 1891: 505, pls 36-37. – Blackburn, 1899: 58, pl. 8. – Hartlaub, 1916: 110, figs 38-39. [all = *C. cocksii*].

? not *Candelabrum verrucosum*. – Schuchert, 2006: 349, fig. 9.

Material examined

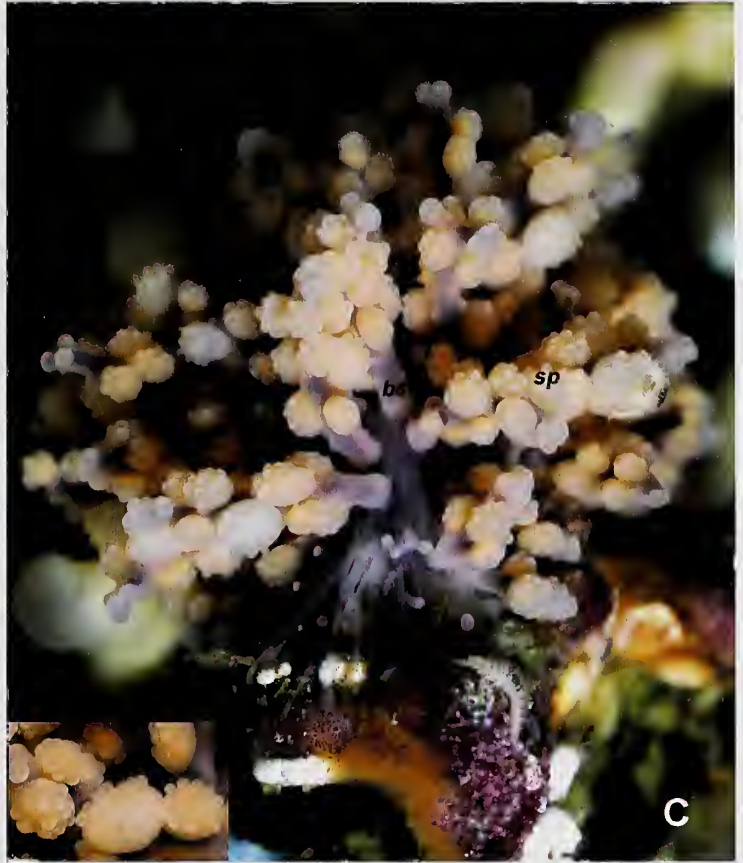
Type material:

Candelabrum verrucosum, UZMO B1376a through B1376g; 7 slides with serial histological sections, labelled “*Myriothela verrucosa*”, from the Norwegian North-Atlantic Expedition. No locality data given. Bonnevie (1899) gives Hammerfest as origin, depth unknown.

Kamchatka material:

MHNG-INVE-92005, field number Kam01; 4 specimens in ethanol, male and female individuals; Russia, Kamchatka Peninsula, Avacha Bay, Starichkov

Fig. 4. *Candelabrum phrygium*, living animals. (A) Whole, semi-expanded polyp, male, size about 3-4 cm. Inset in upper corner: zoom on blastostyles with terminal nematocyst buttons and more proximal sporosacs (Kam08). (B) Semi-expanded polyp in its environment, size 2-3 cm. (C) Basal part of polyp (Kam03) showing attachment-tentacles with sucker-discs and blastostyles with female sporosacs. Inset in lower left: higher magnification of female sporosacs; note the numerous nematocyst buttons on their surface, this specimen has a particularly high number of them, others have fewer. Abbreviations: *sp* = sporosac, *bs* = blastostyle. (D) Basal part of a young polyp (Kam11) with sausage-shaped blastostyles bearing no sporosacs yet and also very few nematocyst buttons only. The blastostyles can easily be mistaken for sporosacs. ►



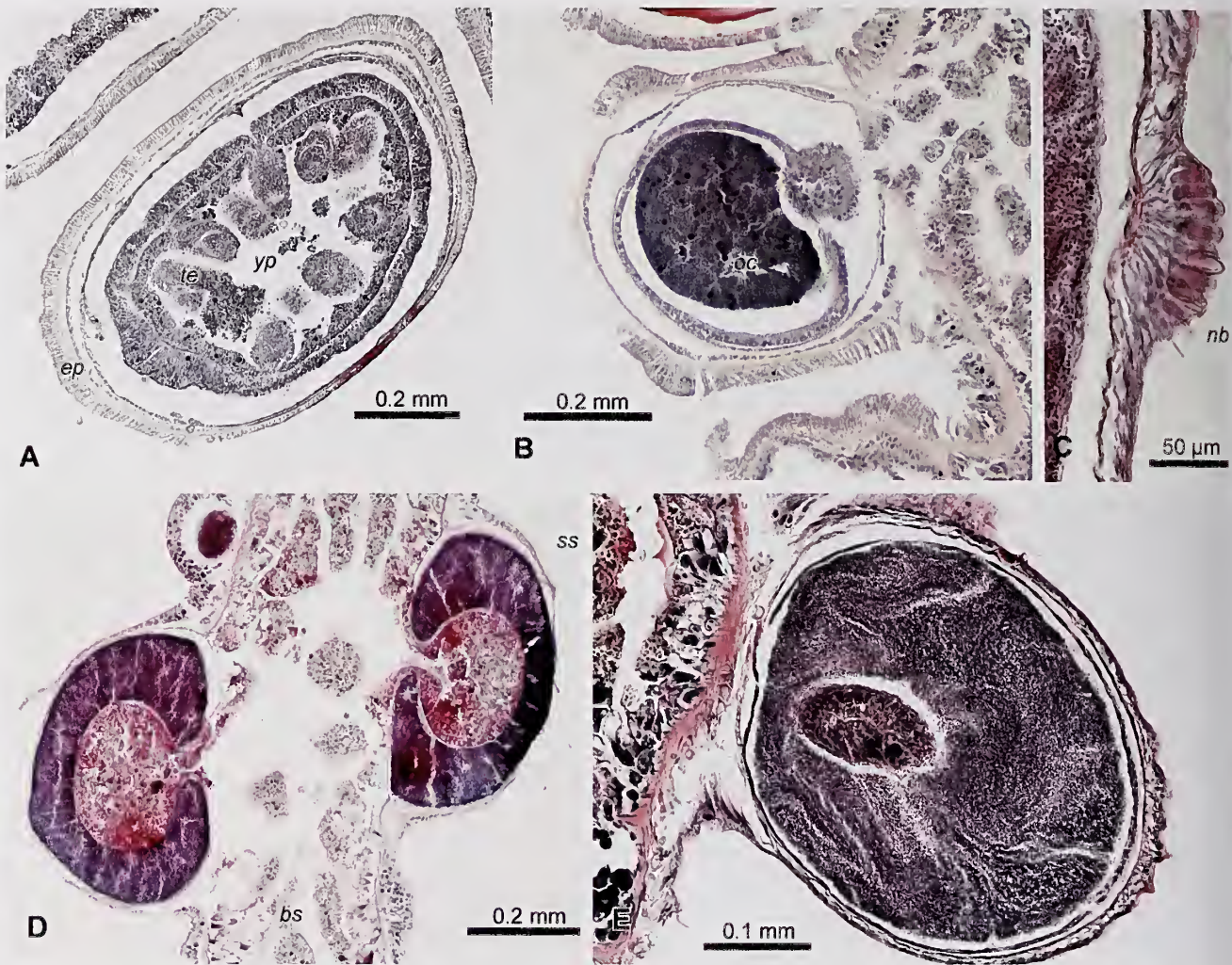


Fig. 5. *Candelabrum phrygium*, histological sections of blastostyles, oriented vertically, males and females originate from different, unisexual individuals, all Kam09. (A) Mature female sporosac with a young polyp (*yp*); *ep* = epidermis of sporosac. Note, the layers of the juvenile are inverted, the tentacles (*te*) directed towards the inside. This inversion is also known to take place in other *Candelabrum* species. (B) Youngest female sporosac observed, *oc* = oocyte. A part of the distal epidermis is lost. (C) Epidermis of a male sporosac with a nematocyst button (*nb*). (D) Two advanced male sporosacs, note the absence of a pedicel or stalk, the sporosacs arise within the epidermal layer, *bs* = blastostyle. (E) Mature male sporosac.

Island, 52.77457°N 158.611517°E, 23 m depth, temperature 0°C; collection date 13.09.2010.

MHNG-INVE-92006, field number Kam02, 3 female specimens in ethanol; Russia, Kamchatka Peninsula, Avacha Bay, Starichkov Island, 52.77457°N 158.611517°E, 23 m depth, temperature 0°C; collection date 13.09.2010.

MHNG-INVE-92007, field number Kam03, 8 specimens, male and female individuals in ethanol and serial histological sections of blastostyles of a male and a female individual; Russia, Kamchatka Peninsula, Avacha Bay, Starichkov Island, 52.77457°N 158.611517°E, 22 m depth, temperature 5°C; collection date 27.07.2010; DNA isolate 1120; 16S sequence LN898139.

MHNG-INVE-92008, field number Kam04, 1 male

specimen in ethanol; Russia, Kamchatka Peninsula, Avacha Bay, Starichkov Island, 52.774783°N 158.61048°E, 23 m depth, temperature 4°C; collection date 27.07.2010.

MHNG-INVE-92009, field number Kam08, 1 male and 1 female individual in ethanol; Russia, Kamchatka Peninsula, Avacha Bay, Bezimenniy Point, 52.84746°N 158.64323°E, 10 m depth, temperature 5°C; collection date 22.07.2009.

MHNG-INVE-92010, field number Kam09, 1 male specimen in ethanol and serial histological sections of 2 blastostyles; Russia, Kamchatka Peninsula, Avacha Bay, Starichkov Island, 52.77457°N 158.611567°E, 20 m depth, temperature 1°C; collection date 13.09.2010.

MHNG-INVE-92011, field number Kam10, 1 male

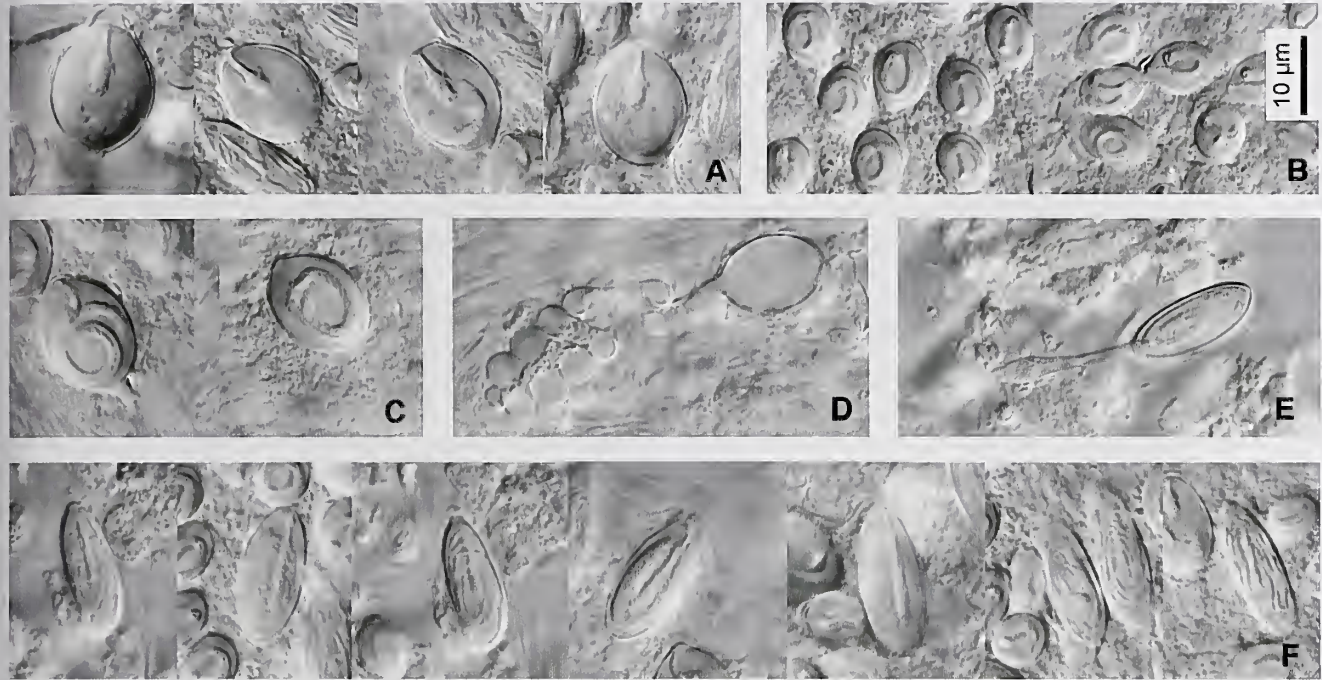


Fig. 6. *Candelabrum phrygium*, nematocysts of preserved animal (Kam12), scale bar valid for all images. (A) Stenoteles. (B) Small desmoneme. (C) Large desmonemes. (D) Discharged large desmoneme. (E) Discharged microbasic eurytele. (F) Microbasic euryteles.

in ethanol and serial histological sections of blastostyle; Russia, Kamchatka Peninsula, Avacha Bay, Starichkov Island, southern side, 52.77367°N 158.61983°E, 24 m depth, temperature 8°C; collection date 26.09.2010.

MHNG-INVE-92013, field number Kam11, 3-4 immature specimens in ethanol; Russia, Kamchatka Peninsula, Avacha Bay, Starichkov Island, behind Karaulny Kekkur, 52.77925°N 158.62348°E, 14 m depth, temperature 12°C, on the shell of a living gastropod *Fusitriton oregonensis*; collection date 27.08.2010; DNA isolate 1122; 16S sequence LN898141.

MHNG-INVE-92012, field number Kam12, 1 male specimen in ethanol; Russia, Kamchatka Peninsula, Avacha Bay, Mayachy Point, rock with sand, 52.88687°N 158.69633°E, 8 m depth, collection date 05.06.2014; DNA isolate 1121; 16S sequence LN898140.

Other Candelabrum phrygium material:

ZMUC-HYD-294; between Iceland and Jan Mayen Island, Ingolf station 117, 69.22°N 08.22°W, 1890 m; collection date 14.07.1896; identification P. Kramp; fragments of very large specimens in ethanol, blastostyles with relatively long tentacles, female sporosacs seen, sessile, without nematocyst buttons.

ZMUC-HYD-295; Greenland; identified by Lütken, collection date unknown; samples mentioned in

Schuchert (2006); 2 female specimens in ethanol and serial histological sections of blastostyles; body size 1-2 cm, rarely nematocyst buttons seen on some sporosacs.

ZMUC-HYD-296; Greenland; much fragmented and not well preserved specimen in ethanol, presumably male, some sporosacs with nematocyst buttons perhaps present.

ZMUC-HYD-297; north of Iceland, Ingolf Station 125, 68.13°N 16.03°W, 1373 m; collection date 29.07.1896; identified by H. Broch; 2 cm specimen in ethanol, blastostyles with tentacles but no sporosacs.

ZMUC-HYD-298; Greenland, Skovfjord, 10-35 m depth; collection date 05.09.1912; identified by P. Kramp; 1 nice specimen on red algae in ethanol, presumably male, some sporosacs with few nematocyst buttons.

ZMUC-HYD-299; between Iceland and Jan Mayen Island; Ingolf station 117, 69.22°N 08.22°W, depth 1890 m; collection date 14.07.1896; identification H. Broch; several black fragments in ethanol, female sporosac seen, no nematocyst buttons.

ZMUC-HYD-300; Greenland, Kap Farvel station 145, 60.07°N 43.20°W, depth 100 m; collection date 27.8.1970; 5 mm specimen in ethanol, juvenile, young sporosacs with or without nematocyst buttons, identity unclear.

Material of previously identified as Candelabrum verrucosum:

ZMUC-HYD-301; southernmost region of Greenland, Kap Farvel Expedition station 148, 60.07°N 43.20°W, 50 m depth; collection date 28.08.1970; 1 cm specimen in ethanol and serial histological sections of blastostyle (Fig. 7C-D), hermaphrodite; sporosacs with up to 10 nematocyst buttons [material mentioned in Schuchert (2006) as *Candelabrum verrucosum*].

Comparison material of Candelabrum cocksii:

MHNG-INVE-36299, 1 specimen in ethanol and histological sections of blastostyles. (see Schuchert, 2006: 341); France, Brittany, Roscoff, 48.73°N 4.00°W, 0 m depth; collection date 17.09.2004.

Type locality: Greenland (Fabricius, 1780).

Diagnosis: Solitary species of *Candelabrum* with polyps 1-10 cm or more in height when reproductive. Basal foot zone relatively short or absent, straight, not sheathed in envelope of perisarc, attached to substratum by tentacle-like filaments, filaments with or without terminal perisarc discs. Numerous blastostyles in part above foot and under tentacle zone, relatively long, 5 mm or more, straight, not branched, with very short capitate tentacles in distal third, often reduced to mere nematocyst buttons; clasper tentacles absent; sporosacs developing in epidermis, without peduncle and thus sessile. Individuals gonochoristic, females viviparous. Distal tentacle zone long and very extensible, with hundreds of short capitate tentacles.

Description of Kamchatka material

Morphology: Polyps solitary, vermiform, size highly variable in being able to expand and contract enormously. Hydranth shape also variable, usually cylindrical to conical, subdivided into distal tentaculate region (trunk), followed by blastostyle region and sometimes also a short foot zone. Foot zone either very short in relation to other parts or absent, not curved, adhering to substratum by several tentacle-like attachment filaments, each with terminal sucker-like ending, the latter sometimes with a disc of perisarc that adheres to substratum, but perisarc discs often absent.

Blastostyle region about 1/4 to 1/3 length of polyp (Fig. 4A), beset by many (>20) simple club-shaped, unbranched blastostyles. Distal end of blastostyles with four to six nematocyst clusters in wart-like

tubercles, number and distribution very variable. Mature blastostyles bearing spherical to hemispherical sporosacs lacking a pedicel, hence sessile (Fig. 5D). Male sporosacs without radial canals, up to 25 per blastostyle at different developmental stages. Female polyps with up to 12 sporosacs per blastostyle, sporosacs without radial canals, eggs fertilized in situ and developing into young polyps, hence viviparous (Fig. 5A, 7C). On surface of sporosacs 1-20 nematocyst buttons, some sporosacs without buttons. All examined polyps unisexual.

Trunk region comprising majority of hydranth length, with numerous (>200) capitate tentacles, these hollow, extensible, capitula oblong.

Dimensions: 1-20 cm in height (maximal size only in situ and when fully expanded), preserved material difficult to assess due to strong contractibility. Blastostyles 5 mm long. Male sporosacs about 0.4-0.5 mm, female sporosacs up to 0.9 mm,

Colours: cream-white, pinkish or orange-yellow.

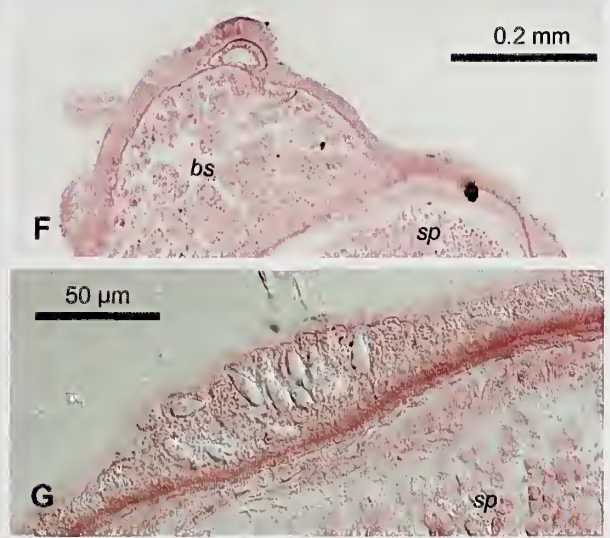
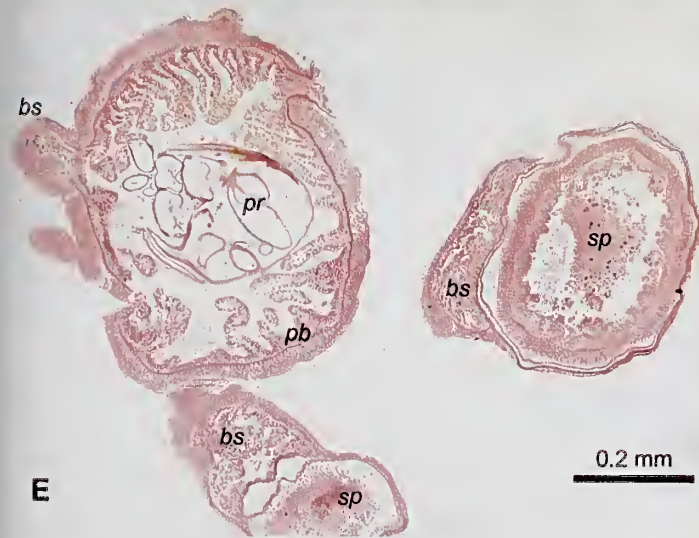
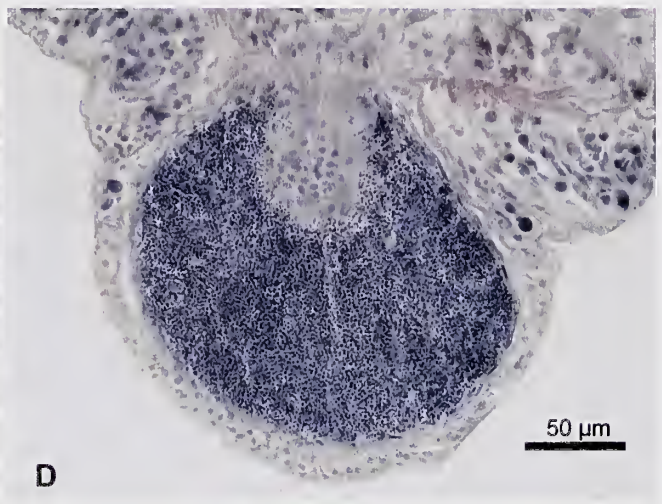
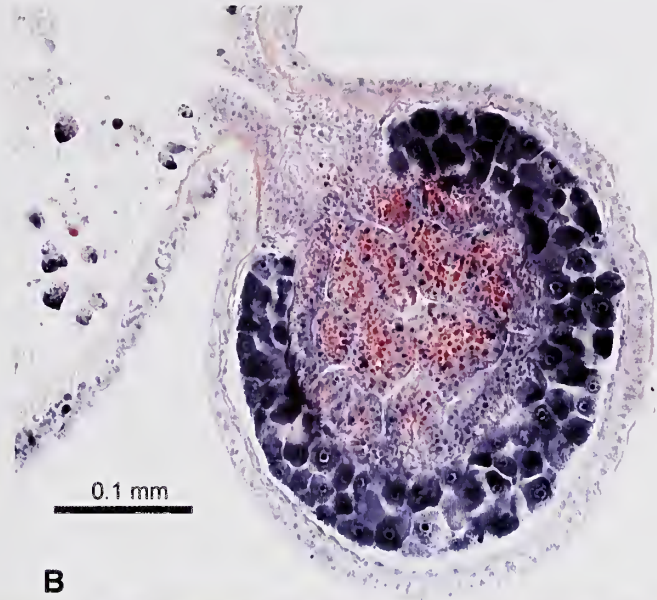
Nematocysts of preserved animals: stenoteles (Fig. 6A), of two size classes, (12.5-16)x(8.5-13.5)µm; small desmonemes (Fig. 6B), (8-9.5)x(5.5-6)µm; large desmonemes (Fig. 6C-D), (14.5-16)x(9-12.5)µm, discharged filament with 5-6 coils; microbasic euryteles with distinctly swollen shaft, shaft somewhat longer than capsule when discharged (Fig. 6E-F), (15-22)x(5.5-8)µm.

Distribution: An Arctic species penetrating into Boreal regions, in the Atlantic waters reaching as far south as the Trondheimfjord (shallow waters) and in deep waters south-west of the Azores (Schuchert, 2006). It has also been recorded in the Russian Arctic seas and the northern Pacific (Paramushir Island, south of Kamchatka Peninsula; Naumov, 1969). (Note that numerous other records under this name from coastal regions of the NE Atlantic refer actually to *Candelabrum cocksii*; see Schuchert, 2006.)

Biology: Occurs usually at considerable depths of several hundreds of meters down to 2195 m (Bonnievie, 1899), but in the high Arctic it has been found as shallow as 13 m (Jäderholm, 1908). The current findings from Kamchatka confirm that it also occurs in shallow (8-23 m) depths.

The polyps live permanently attached to solid substrata like rock, bivalves, hydroids, bryozoans, and algae. The present material was found on stones and frequently

Fig. 7. (A-B) *Candelabrum cocksii*, longitudinal sections of sporosacs of the same blastostyle, MHNG-INVE-36299. (A) Mature male sporosac. (B) Young female sporosac with many differentiating oocytes. (C-D) *Candelabrum* spec. from Greenland, ZMUC-HYD-300, hermaphrodite, longitudinal section of a single blastostyle and its sporosacs. (C) Left a female sporosac with young polyp (tentacles inverted), adjacent a small, developing male sporosac with maturing spermatozooids. (D) Small male sporosac with spermatozooids of an advanced stage. (E-F) *Candelabrum verrucosum*, holotype. (E) Horizontal section in region of blastostyles. (F) Blastostyle with developing tentacle (top). (G) Nematocyst button on sporosac. Abbreviations: *bs* = blastostyle, *pb* = polyp body, *pr* = prey item, *sp* = sporosac. ►



on the bryozoan *Myriopora orientalis* (Fig. 4B). Two young specimens (Kam11) were found on the shell of a living gastropod *Fusitriton oregonensis* (Redfield).

Like other *Candelabrum* species, *C. phrygium* is viviparous and lacks a planula phase (Sars, 1877; Schuchert, 2006). The newly released polyp is spherical and has 20-30 capitate tentacles. The tentacles formed while the embryos is still in the sporosac develop inverted into the gastric lumen (Fig. 5A), but they revert to the outside before hatching (comp. Allman, 1876; Schuchert, 2006).

Remarks: All *Candelabrum* species have been reviewed by Segonzac & Vervoort (1995), but many remain difficult to separate if no biogeographic information is considered. The Kamchatka material conforms well to existing descriptions of the Arctic *Candelabrum phrygium* (e. g. Segonzac & Vervoort, 1995; Schuchert, 2006), except for the presence of nematocyst buttons on the sporosacs (Figs 4C, 5B-C). These buttons occur in variable numbers from 1 to 20 per sporosac, and occasional sporosacs also lack them. The presence of such nematocyst buttons has been deemed diagnostic for the species *Candelabrum verrucosum* (Bonnievie, 1898) (Segonzac & Vervoort, 1995; Schuchert, 2006), but a re-evaluation is necessary. *Candelabrum verrucosum* is a very rare, poorly described species. After examining the type material, Rees (1956) considered it conspecific with *C. phrygium*. Segonzac & Vervoort (1995) kept it distinct, but had no new material. The only specimen-based record of *C. verrucosum* after the first description was that of Schuchert (2006). The identification of his Greenland specimen relied on the presence of nematocyst buttons, which were presumed to be diagnostic for the species. The simultaneous presence of both male and female sporosacs (Fig. 7C) distinguished the sample clearly from the *C. phrygium*, which is gonochoristic (Segonzac & Vervoort, 1995).

However, the identity of *C. verrucosum* warrants reappraisal. Bonnievie's (1898) description of the species was cursory, and suitable illustrations were not provided. Bonnievie mentioned the presence of flat radial canals in the gonophores, which would be quite unusual for the genus (comp. Briggs, 1928, 1929, 1931; Manton, 1940). Moreover, there was a small gastrodermal vesicle (depicted in Bonnievie, 1899: pl. 4 fig. 2a) under the nematocyst buttons of young sporosacs in Bonnievie's material, something never seen in the present material and also not observed in the material of Schuchert (2006; see Fig. 7C-D). Another error in the original description seems likely, as Bonnievie (1898) stated that the essential diagnostic trait of the species was the existence of nematocyst buttons on the blastostyle, while in the preceding paragraph she described them as being on the gonophores. In the following section she described more histological details, but referred to the blastostyle instead of a gonophore. In order to get a clearer picture,

it was thus necessary to re-examine the type material of *C. verrucosum*, obtained on loan from the Natural History Museum of Oslo University. The type material was not labelled as such, but there can be no doubt that this is what remains from the holotype of *C. verrucosum*. The material is apparently from the "N. Nordhavsekspedition" and is clearly labelled as *Myriothela verrucosa*; moreover, Bonnievie (1898) stated that she made histological sections. The material consists of seven microscope slides with stained, serial histological sections. The slides are marked with a letter ranging from a through g. The tissues are not well preserved, something already deplored by Bonnievie (1898: 487), and it takes some effort to identify what is present on the slides (Fig. 7E). The presence of the tentacle zone in the last slides and the presence of a prey item in the gastric system permit an identification and orientation of the sectioned parts. Slides a-f contain horizontal sections of the whole polyp ranging from the blastostyle region (Fig. 7E) to the beginning of the tentacle zone. Slide g, in contrast, contains serial longitudinal sections of a blastostyle with two sporosacs. The slides allow corrections and additions to be made to Bonnievie's account:

- there is no evidence of male sporosacs; all appear to be female, the most advanced containing a young polyp with inverted tentacles, so the animal is thus likely gonochoristic.
- there are only very few nematocyst buttons on the sporosacs (Fig. 7G) and there is no gastrodermal vesicle below it. The situation is identical to that seen in the new material (Fig. 5C).
- sporosacs have no radial canals or any vestiges of them.
- the nematocyst buttons and the underlying "small gastrodermal vesicles" depicted in Bonnievie (1899: pl. 4 fig. 2a; here 7F) most likely represent a small tentacle on the blastostyle (the "small gastrodermal vesicle" is in fact the lumen of the tentacle). The vesicles definitely do not occur on mature sporosacs (Fig. 7G).

From a re-examination of the type material of *C. verrucosum* and other historical material of *C. phrygium*, we conclude that there is no evidence to warrant separation of the two species. As already concluded by Rees (1957), *C. verrucosum* must be regarded as a synonym of *C. phrygium*.

Re-examination of material of *C. phrygium* from the ZUMC revealed that historical samples of the species (see material examined) may also have occasional nematocyst buttons on the sporosacs, but never as many as seen in some females of specimens from Kamchatka. The sole presence of these nematocyst buttons is thus not diagnostic for *C. verrucosum*. The possible developmental origin of nematocyst buttons in Kamchatka material is also important in this context. The gonophores develop from cell aggregations at the base of the epidermis as described for *C. penola* by Manton (1940: fig. 3). In

contrast to *C. cocksii* (Fig 7A-B), no stalk develops and the sporosacs remain sessile (Fig. 5B-D) while the original blastostyle epidermis stretches over them. The blastostyles may also bear at their end short capitate tentacles or mere nematocyst buttons (comp. Fig. 4A or Schuchert, 2006: fig. 8B). These tentacle rudiments may end up on the surface of a growing sporosac, possibly explaining their occasional presence. However, the large numbers seen here (e. g. Fig. 4C) are clearly an additional development. Although certainly not enough material has been examined for a well-founded conclusion, it is interesting to note that only colonies from shallow waters (7-50 m) had numerous buttons, while deep water specimens had none or only a few. This can of course also be used as an argument to separate the two groups into two distinct species, but we prefer to think that the number of nematocyst buttons is environmentally related, e. g. induced by unspecific predators/browsers like nudibranchs, which are presumably more abundant in shallow waters. We therefore consider the presence of nematocyst buttons alone as insufficient justification to regard *C. verrucosum* as distinct, and the Kamchatka material is assigned to *C. phrygium*. The high number of nematocyst buttons on female sporosacs is here considered to constitute intraspecific variation or to be environmentally induced. Moreover, *Candelabrum phrygium* has already been recorded from the region by Naumov (1969, Paramushir Island).

If presence of nematocyst buttons on the sporosacs is insufficient basis to distinguish *C. verrucosum* as a valid species, then the identification of Schuchert (2006) of a Greenland specimen as *C. verrucosum* has to be revised. This material is clearly hermaphroditic (Fig. 7C) and thus different from all known samples of *C. phrygium*. So far, only two hermaphroditic species of *Candelabrum* are known, namely *C. cocksii* and *C. serpentarii* Segonzac & Vervoort, 1995. *Candelabrum cocksii* is a distinct species, easily separable by its characteristic clasper tentacles which hold the encapsulated developing embryos (Schuchert, 2006). *Candelabrum serpentarii*, on the other hand, differs only from *C. phrygium* in being hermaphroditic (Segonzac & Vervoort, 1995). Note that size differences in *Candelabrum* are of minor importance as reproductive animals can vary in size by an order of magnitude (e. g. *C. penola*, Manton, 1940). Likewise, the nematocyst types are rather uniform and any observed differences are of little use for the few, allopatric specimens that are available. Photographs of the type specimen of *C. serpentarii*, kindly provided by Dr A. Andouche (Muséum National d'Histoire Naturelle, Paris), showed no evidence of nematocyst buttons. Some of the sporosacs contain young polyps, while others are smaller and opaque. Without histological sections it is impossible to determine their sex. Segonzac & Vervoort (1995) apparently did not make histological sections, and their interpretation that the animal is hermaphroditic needs reconfirmation. Nevertheless, it could be that also hermaphroditism is part of the intraspecific variability of

C. phrygium (perhaps it is a sequential hermaphrodite) and this has not been seen due to the small number of specimens examined histologically.

To clarify species limits within the genus *Candelabrum*, and to settle the identity of specimens examined here, more samples of these rare species are needed and additional molecular genetic analyses must be undertaken. The three 16S sequences of the Kamchatka material obtained here are minimally different, and BLAST searches in GenBank (results not shown) gave as the closest match *Candelabrum austrogeorgiae* (accession number FN424120). Unfortunately, insufficient data are currently available from other species for a more detailed taxonomic assessment.

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